Title: Combining abundance and performance data reveals how temperature regulates coastal occurrences and activity of a roaming apex predator

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Abstract

The redistribution of species has emerged as one of the most pervasive impacts of anthropogenic climate warming, and presents many societal challenges. Understanding how temperature regulates species distributions is particularly important for mobile marine fauna such as sharks given their seemingly rapid responses to warming, and the socio-political implications of human encounters with some dangerous species. The predictability of species distributions can potentially be improved by accounting for temperature's influence on performance; an elusive relationship for most large animals. We combined multi-decadal catch data and bio-logging to show that coastal abundance and swimming performance of tiger sharks *Galeocerdo cuvier* are both highest at ~22°C, suggesting thermal constraints on performance may regulate this species' distribution. Tiger sharks are responsible for a large proportion of shark bites on humans, and a focus of controversial control measures in several countries. The combination of distribution and performance data moves toward a mechanistic understanding of tiger shark's thermal niche, and delivers a simple yet powerful indicator for predicting the location and timing of their occurrences throughout coastlines. For example, tiger sharks are mostly caught at Australia's popular NSW beaches (i.e. near Sydney) in the warmest months, but our data suggest similar abundances will occur in winter and summer if annual sea surface temperatures increase by a further 1-2°C.

Introduction

Exploring the influence of temperature on species' distributions has a long history in ecology, and a focus on temperature-dependent biogeography has intensified in recent decades with concerns over a warming climate. Distributions of marine animals appear to be responding more rapidly to climate change than are those of terrestrial animals (Sorte *et al.*, 2010), and this is particularly the case for mobile and broadly distributed species (Sunday *et al.*, 2015)

such as many sharks. Understanding and predicting distribution shifts in sharks is increasingly important given their declining global abundances (Ferretti *et al.*, 2010), the consequences of such declines for top-down control of ecosystems (Ferretti *et al.*, 2010), and the socio-political implications of human encounters with some potentially dangerous species in coastal areas.

Among biogeographers, a central and commonly-posed question (e.g. Buckley *et al.*, 2010; Davis *et al.*, 1998; Kearney & Porter, 2009; Thomas *et al.*, 2004) is how well models predict future species distributions when they are parametrised solely by identifying correlations between distributions of organisms and environmental conditions. It is increasingly recognised that predictions can be refined by incorporating measured relationships between environmental conditions (e.g. temperature) and organism performance (e.g. locomotion or feeding) because doing so can reveal the proximate constraints limiting distributions (Kearney & Porter, 2009). These so called 'mechanistic models' have been influential in predicting distributions of broad taxa, including terrestrial arthropods, lizards and amphibians (e.g. Buckley, 2007; Kearney *et al.*, 2008; Kearney & Porter, 2004). Due to difficulties associated with measuring performance of large marine animals such as sharks, our understanding of how temperature regulates their distributions is based almost exclusively on correlations between environmental temperature and relative abundance. Potential limitations of these correlative approaches are exacerbated by the often geographically disparate nature of tagging and bycatch studies that form the basis of our knowledge of current shark distributions.

Tiger sharks *Galeocerdo cuvier* are large ectothermic apex predators distributed throughout the world's tropical, subtropical and warm-temperate oceans. Tracking studies have implicated temperature as a driver of their movement in Australia (Ferreira *et al.*, 2015; Holmes *et al.*, 2014), Hawaii (Papastamatiou *et al.*, 2013), and the Northwest Atlantic (Lea *et*

90 *al.*, 2015), and catch data suggest coastal abundance responds to temperature variation in several regions (Dicken *et al.*, 2016; Heithaus, 2001; Reid *et al.*, 2011). Nevertheless, like
92 most shark species, a combination of tiger sharks' broad distribution, low relative abundance, and the geographically discrete nature of published studies have precluded a clear
94 understanding of the thermal ecology of this species. They can be variously considered ocean-scale migrants (Lea *et al.*, 2015) or perennial island residents (Fitzpatrick *et al.*, 2012;
96 Meyer *et al.*, 2010), and individuals inhabit a broad variety of thermal niches. Our poor ability to predict when and where tiger sharks will occur is a particularly important problem
98 given they are responsible for the highest number of recorded human fatalities after white sharks *Carcharodon carcharias,* and are currently a key focus of controversial bather
100 protection programs (including culling) is several countries (e.g. Dicken *et al.*, 2016; Holmes *et al.*, 2012). Development of simple indicators (such as water temperature) that can reliably
102 predict when and where sharks are most likely to occur could represent powerful tools both for forecasting ecological consequences of range shifts with future warming and for
104 maximising the efficacy of bather protection programs. Approaches that additionally account for temperature's influence on performance of sharks should be more powerful and
106 potentially more robust than those based solely on correlative distribution data (Davis *et al.*, 1998; Kearney & Porter, 2009). Recent advances in bio-logging technology have provided
108 new possibilities for measuring performance of large marine organisms, and a potential means of deriving performance proxies from animals with which laboratory experimentation
110 is difficult. For example, accelerometers quantify mechanical work done by animals (Gleiss *et al.*, 2011; Wilson *et al.*, 2006), and have shown promise as a tool for measuring
112 temperature's influence on locomotor performance in several wild estuarine fish species (Gannon *et al.*, 2014; Payne *et al.*, 2016).

If the likely increases in sea surface temperate over the coming decades are to see a corresponding shift in the distributions of tiger sharks, predicting the location and timing of such shifts could be valuable for ecologists and managers alike. In this study, we combined relative abundance and physiological performance data to explore how temperature regulates the distribution of tiger sharks. First, we compiled a spatially extensive (spanning ~ 18° of latitude along Australia's eastern coast), multi-decadal dataset on tiger shark coastal catch rates, and by pairing catch data with high resolution temperature records estimated how temperature influences tiger shark relative abundance. Next, we used animal-borne accelerometers to measure dynamic body activity (a proxy of swimming performance) of tiger sharks as they swam freely in their environment, and determined how swimming performance varies with water temperature. Our aim was to understand how temperature influences both the broad scale distribution patterns of tiger sharks and their physiological performance, thus enabling more robust (Kearney & Porter, 2009) predictions about how populations of this species will respond to future warming.

Methods

Catch data

As a proxy of tiger shark relative abundance, we used multi-decadal records of sharks caught in coastal areas along Australia's eastern coastline by government shark control programs. Data from the Queensland shark control program (QSCP) were provided by the Department of Agriculture and Fisheries, Queensland Australia, for the period spanning May 1996 to December 2015. A detailed description of the program can be found in Holmes et al (Holmes *et al.*, 2012). Briefly, the QSCP deploys mostly baited drum lines and some nets approximately 500-1000 m from shore adjacent to 85 popular bathing locations across the state. Fishing contractors check gears at least every second day (average of 15-20 days per

month) and record information including gear type, species, total length, and since mid-1996, the temperature of surface waters immediately adjacent to captured sharks. New South Wales (NSW) adjoins the southern extent of the QSCP, and a shark netting bather protection program has been operating in NSW since 1949, with nets currently deployed off 51 beaches across the State. These nets are set every weekend day and 9 weekdays per month, however since 1987 the program has excluded winter months (Reid *et al.*, 2011). A previous paper (Reid *et al.*, 2011) reported the percentage of tiger shark catches reported across the NSW shark netting program per calendar month from 1950 to 1982 (a period where within-year effort has remained constant), so we included those data in our analysis.

Standardisation of catch data

Within each location, the number of deployed drum lines and nets have remained relatively constant since 1993, particularly within years (Holmes *et al.*, 2012), whereas the number and type of gears varies by location, as do factors such as distance of gears from shore, bait type, and local bathymetry (Holmes *et al.*, 2012). Given these complexities, we chose not to compute metrics such as 'catch-per-unit-effort (CPUE)' for testing temperature's influence on catches across locations, and instead examined relative trends in catch between months within locations. Because sampling effort and site effects have remained constant within years at each location over the 20-year sampling period, for the QSCP, we computed the percentage of total catches of tiger sharks reported per calendar month at each location across the period spanning 1996-2015, and paired these monthly data to mean catch temperatures (temperatures recorded at the location and timing of each captured shark by the fishing contractors) per calendar month at those locations (i.e. all data pairs from the 20 years were grouped into one of 12 months). This removes the difference in magnitude between location, and allows us to explore relative trends with temperature. Water temperatures are not recorded on location for the NSW program, so we paired monthly percentage catch data to

mean monthly SSTs collected by the Australian Government's Meteorology and Oceanography Hydrographic Service (www.metoc.gov.au). Monthly SST was measured within 10km of Sydney's coast (33.5°S), and averaged over a 10-year period (2006-2015). The added benefit of using '% catch' is that we can also include different gear types (i.e. baited hooks and nets) into the analysis – this is not possible with CPUE data. Subsequent analyses were based on these location-specific percentage catch data. Consequently, catch results reflect absolute monthly differences in catch within locations, but not between locations. To estimate the temperature coinciding with highest catches across both the QSCP and the NSW program, we grouped tiger shark catch and temperature data for each calendar month into four latitudinal zones (16-19, 21-25, 26-28 and 33-34°S), and fitted a two-part thermal performance curve of the form

$$A = \begin{cases} S \times e^{-\left(\frac{T - T_{opt}}{2\sigma}\right)^2} & for\ T \le T_{opt} \\ S\left(1 - \left(\frac{T - T_{opt}}{T_{opt} - T_{crit}}\right)^2\right) & for\ T > T_{opt} \end{cases}$$

where A is percentage catch, T_{opt} is the temperature (T) at which catch rate is maximised, σ is the standard deviation for the normally distributed half of the curve, T_{crit} is the high temperature where A is zero, and S is a scalar. Curves were fitted using minimum least squares non-linear regression in the program *R* (R-Core-Team, 2016). Because our shark-temperature data were presence-only (water temperature was only recorded when sharks were caught), we also built thermal performance curves using the (catch-independent) Metoc coastal SST data, which were all 10-year monthly averages and with SST recorded within 50km of the coastline at each drum-lining location.

Rather than exploring the role of location, or to create a predictive model to calculate absolute catch of tiger sharks, the goal of our analysis is to identify the shape of the relationship between temperature and catch, and particularly to identify a T_{opt}. Because catches of tiger sharks were reasonably uncommon, we summed monthly across years in each zone to improve our ability to generalise the temperature-catch relationship. By creating samples that span a number of years and locations (within zones), we give ourselves the greatest power to detect differences between our factors of interest (temperature, and geographical region). As a means of validating our percentage catch approach, we conducted several additional analyses. First, we tested for spatial and temporal dependency by fitting a generalised additive model (GAM) and generalised additive mixed model (GAMM) to the tiger shark percentage catch data. The GAM included a smoother for 'temperature', and the GAMM included an additional cyclic smoother for 'month', and an autoregressive term (AR1) for 'month' nested in 'zone'. These models were fitted using the 'mgcv' R package (Wood, 2011, 2017). Second, we used a subset of the catch data (including only drumline data [which excludes all NSW data], and only months where 'effort' was reported; see Holmes *et al.*, 2012) to compute CPUE, which we modelled with a GAM, using a smoother of 'temperature' and with 'zone' (3 levels) as a fixed factor. There was no residual serial correlation (evaluated using the 'acf' autocorrelation function in R) so this GAM excludes temporal dependency terms.

For comparison with tiger sharks, we also computed monthly percentage catch and temperature data (as for tiger sharks) for other shark species reported in the QSCP and NSW programs that are known to have biogeographies different to tiger sharks; these were the cool-water white shark *Carcharodon carcharias* and the tropical blacktip shark *Carcharhinus limbatus* (due to imperfect species identification by contractors, it is likely that reports of "blacktip sharks" include some contribution of *C. tilstoni* and *C. melanopterus*, but since all

three blacktip species are characterised by tropical distributions, a blacktip complex serves as a useful comparison to the temperature dependence of catches of tiger and white sharks, with those species having quite different biogeographies).

Bio-logging and telemetry

Overall dynamic body acceleration (ODBA; Gleiss *et al.*, 2011; Wilson *et al.*, 2006) is a proxy of mechanical work done by animals, and generally well-correlated with rates of energy expenditure (Halsey *et al.*, 2009; Payne *et al.*, 2011). Recently, ODBA has also been shown to vary strongly with temperature in wild fishes and in a manner consistent with theoretical expectations (Angilletta, 2009) of thermal performance curves (Gannon *et al.*, 2014; Payne *et al.*, 2016). Because temperature's influence on physiological performance generally cannot be measured in controlled environments for large shark species (Payne *et al.*, 2015), we measured ODBA of tiger sharks swimming freely in the wild. When measured in the wild, ODBA does not directly measure variation in physiological performance 'capacity', but rather the combination of intrinsic physiological constraints and behavioural decisions made in a dynamic environment (see Payne *et al.*, 2016). Since both intrinsic physiology and behaviour are central parameters for improving mechanistic understanding of species' niches (Kearney, 2006), we considered measuring temperature's influence on ODBA of wild sharks to be a useful approach to understanding thermal limitation of their performance. Throughout October and November 2011, five tiger sharks (247-387 cm total length, three female and two male) were instrumented with accelerometer packages on the dorsal fin off the east coast of Oahu, Hawaii (~ 21.5°N, 157.75°W), with full details of tagging reported in Nakamura et al (Nakamura *et al.*, 2011). After release, tri-axial acceleration, depth and temperature were recorded for between 14 h and 7.4 days (mean of 2.9 days per shark), with acceleration sampled at either 8 or 16 Hz, and both depth and temperature sampled at 1Hz. The static component of acceleration was filtered from each axis

using established methods (Sato *et al.*, 2003) in order to compute ODBA. We then resampled
236 the full ODBA record to only retain values coinciding with the temperature measurements recorded at 1Hz. For each deployment, mean ODBA was calculated per 0.1°C bin after a
238 recent study reporting the thermal sensitivity of ODBA in several fishes (Payne *et al.*, 2016). Because small differences in accelerometer placement and shark size can influence absolute
240 acceleration measurements, we rescaled all mean bin data to a range of 0-1 for each shark, and then calculated the grand mean ODBA per 0.1°C for the five sharks combined. We
242 excluded bins where fewer than 20 ODBA readings were provided per bin per individual (corresponding to < 20 seconds of ODBA data) to reduce the influence of temperature bins
244 that were encountered very infrequently, and mean ODBA values that were unlikely to represent steady-state swimming. To estimate the temperature at which ODBA is greatest, we
246 fitted the two-part performance curve as above, where *A* is ODBA. While we used the same approach to generating a thermal performance (ODBA) curve as Payne et al. (2016),
248 differences in the resolution of accelerometer data (≥ 1 Hz versus < 0.01 Hz in the earlier paper), monitoring durations (days versus months), and species' ecologies (large negatively-
250 buoyant sharks transiting through broad depth ranges versus small-bodied benthic and demersal teleosts) demand caution when directly comparing parameters of the thermal
252 performance curves between this study and that of Payne et al. (2016).

The accelerometer loggers recorded ambient water temperature, and since the
254 instrumented sharks were large, their core body temperatures were probably sometimes different to ambient temperatures (Sato, 2014). To examine how tiger shark movement
256 varies with body temperature, we internally implanted tiger sharks with temperature sensors and used acoustic telemetry to compare tiger shark body temperature to the time they spent in
258 coastal regions of Hawaii. We felt that measuring the combination of how ambient temperature influences swimming performance and how body temperature influences coastal

movement for the same population of tiger sharks provided a good overview of temperature's influence on behaviour and activity of these animals. In October 2013, acoustic transmitters containing a temperature sensor (Vemco V16T) were implanted into the peritoneal cavity of four female tiger sharks (310-413 TL). These transmitters recorded body temperature and transmitted measurements approximately every 3 min. Time-stamped body temperature records and shark movements were monitored via an array of 14 acoustic receivers (Vemco VR2W) deployed around the coast of Maui (Hawaii). Receivers were all deployed off the western half of the island, with seven of them within 700m of the coast and the other seven within 5 km of the coast. The deepest receiver was in ~ 90m water depth, with most receivers in < 50m depth. Inshore receivers were deployed at high recreational use (i.e. swimming, snorkelling and surfing) sites, including locations of recent shark bite incidents. The Maui acoustic array is part of a broader array spanning the Hawaiian Islands operated by the University of Hawaii (for details see Meyer *et al.*, 2010; Papastamatiou *et al.*, 2013), with the detection range of receivers measured at up to 950m (Meyer *et al.*, 2010), and thus a maximum horizontal monitoring area of ~ 2.8 km^2 per receiver. Because the absolute frequency of acoustic detections is not always a reliable indicator of marine animal residency (Payne *et al.*, 2010), we calculated the total number of hours that each shark was detected (using a threshold of > 2 detections per hour to deal with potential 'false detections') at any of the coastal receivers in each calendar month , and expressed each monthly value as a percentage of the total number of hours detected per shark. To give equal weight to each shark, we then calculated the mean monthly percentage of hours detected across the four sharks. Second order polynomial regression was used to compare mean body temperature (recorded by the acoustic receiver array) per month to the percentage of time spent at Hawaiian coastal receivers per month.

Results

Coastal catch rates

A total of 4,750 records of historical tiger shark catches were obtained over ~ 18° of latitude along Australia's eastern coast (Cairns [16.9°S 145.8°E] to Wollongong [34.5°S 150.9°E]) and a period spanning 1950 to 2015. The size of sharks ranged from 0.5 to 5.5m TL. Sex was often not reported, but 61% of sexed sharks were female. Most records were of tiger sharks caught on baited drumlines off Queensland, with 4,566 sharks and corresponding measurements of water temperature reported from 1996 to 2015 in that State. Only 184 tiger sharks were caught by the New South Wales bather protection program from 1950 to 1981 (Reid *et al.*, 2011). Stratifying catches in each of four latitudinal zones into each calendar month showed that the percentage of catches in each zone varied markedly with temperature (Fig. 1a). Tiger shark catches were highest during the coolest months in the northern tropical zone (16 – 19°S), but highest during the warmest months in the southernmost zone (33 – 34 °S). The seasonality of catches in each zone suggested a consistent trend towards catches being highest in coastal water temperatures of ~ 22°C regardless of latitude (fitting of a two-part thermal performance curve to all monthly catch data in the four zones returned a T_{opt} estimate of 21.6°C and 95% CIs of 20.1 – 23.1°C; σ = 2.37, S = 10.09, T_{crit} =31.75; $P < 0.05$, R^2 = 0.37; Fig. 1a). Use of the independent coastal SST dataset gave very similar results (T_{opt} = 22.4°C, 95% CIs of 19.9 – 24.3°C; σ = 2.9, S = 9.7, T_{crit} =31.3; $P < 0.05$).

Both the GAM and GAMM spines for the % catch data were highly significant (P = 0.0001 and 0.002, respectively) and almost identical, with T_{opt} ~ 22°C (as with our 2-part curve; Fig. S1). The small amount of residual autocorrelation had little impact on the relationship between temperature and % catch (Fig. S1, Table S1), suggesting the domed pattern shown in Fig. 1 is reliable. For the reduced CPUE dataset, absolute CPUE varied between the three zones, but the GAM including zone as a factor returned a domed

310 relationship between CPUE and temperature ($P < 0.05$), with a $T_{opt} \sim 22°C$ (as with all other analyses; Fig. S2, Table S2).

312 The higher catches of tiger sharks near 22°C were in stark contrast to the relationships between coastal water temperature and catch rates for shark species with different

314 biogeographies that were caught throughout Queensland (as reported by the bather protection program in that State); e.g. catches of the tropically-distributed blacktip shark *Carcharhinus*

316 *limbatus* continued to increase up to the warmest temperatures encountered in coastal areas (28-29°C; Fig. 1b), whereas catches of the regionally-endothermic white shark *C. carcharias*

318 were highest at cooler temperatures (~ 19°C or lower; Fig. 1c), with a complete reduction in catches coinciding with the temperature of the endothermic muscles (~ 26°C) of that species

320 (Goldman, 1997) (note: two-part performance curves could not be fitted to catch data for *C. limbatus* and *C. carcharius*, so we fitted fourth-order polynomial curves to those data for

322 graphical purposes; Fig. 1 dashed lines. Best-fit model for *C. limbatus*: $y = -0.0012x^4 + 0.1072x^3 - 3.6185x^2 + 55.231x - 321.24$; *C. carcharius*: $y = -0.02135x^4 + 2.015x^3 - 70.65x^2$

324 $+ 1089x - 6198$).

The ratio of winter to summer (Dec-Feb and Jun-Aug respectively) catches decreased

326 strongly with increasing latitude (least-squares linear regression on ratios from the 27 locations from which at least one tiger shark was captured in summer and winter; $F_{1,25} =$

328 44.5, $P < 0.0001$); tiger shark catches were approximately three times higher in winter than in summer at the equatorward limit of the sampling region, but catches were twice as high in

330 summer as in winter in the southern regions (i.e. around Sydney [34°S] ; Fig. 2). This shifting seasonality of tiger shark catches with latitude reflected their higher catches in water

332 temperatures of ~ 22°C, with the change from higher catches in winter to summer occurring at latitudes where mean annual sea surface temperatures (SSTs) are in the range of 22-23°C

334 (Fig. 2).

336 *Bio-logging*

A thermal performance curve fitted to the relationship between ODBA and water temperature
338 was somewhat variable over the ~14°C temperature range that the sharks encountered (~13–
27°C), but data returned a T_{opt} of 21.2°C and 95% CI of 18.8 – 24.0°C; σ = 3.92, S = 0.22,
340 T_{crit} = 29.0°C; Fig. 3a (note: the T_{crit} estimate does not indicate that the sharks were motionless at 29°C; ODBA data were rescaled to the range of 0-1, so T_{crit} was the
342 temperature coinciding with the minimum ODBA values recorded during the study).

From October 2013 to June 2015 we recorded 4806 internal body temperature
344 readings from the four transmitters (1986, 1244, 864 and 712 readings from 282, 163, 121 and 69 different hours, respectively), with all sharks detected relatively consistently across
346 the 33-month monitoring period. The sharks were detected more frequently in coastal regions of Hawaii when their body temperatures were lowest (the coolest SSTs in Hawaii throughout
348 the year are in the region of 24°C), and less frequently in those regions when their body temperatures increased (Fig. 3b). Internal body temperatures of those sharks were very
350 similar to SSTs whenever they were in coastal shelf habitat (85% of mean hourly body temperature readings were within ± 1.0°C of SSTs throughout the 30 month monitoring
352 period; Fig. S3). The range of coastal SSTs experienced by the acoustically-tagged Hawaiian sharks (Fig. S3) was similar to the range of coastal temperatures over which tiger sharks were
354 caught in the northernmost zone in Australia (Fig. 1a).

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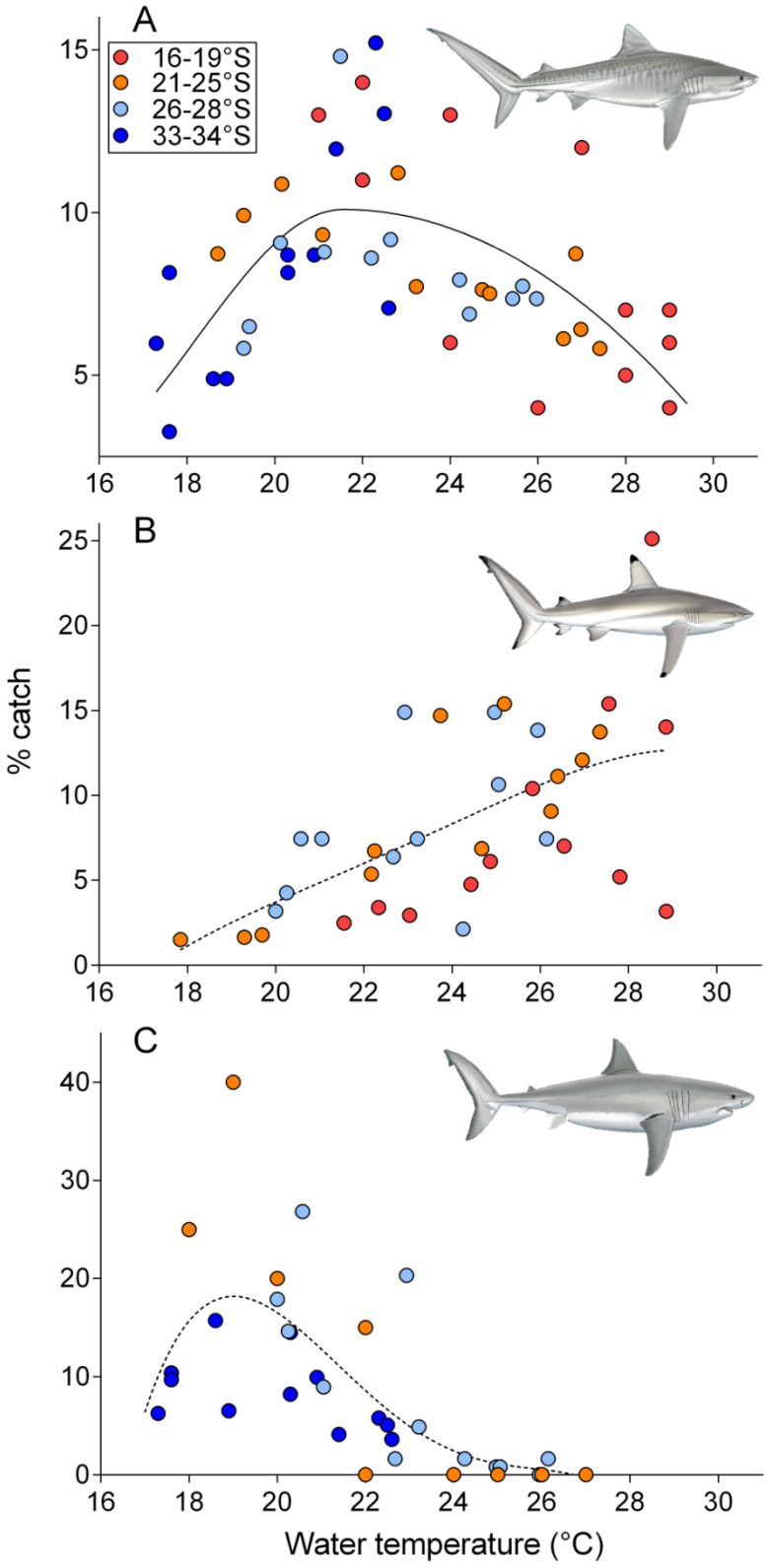
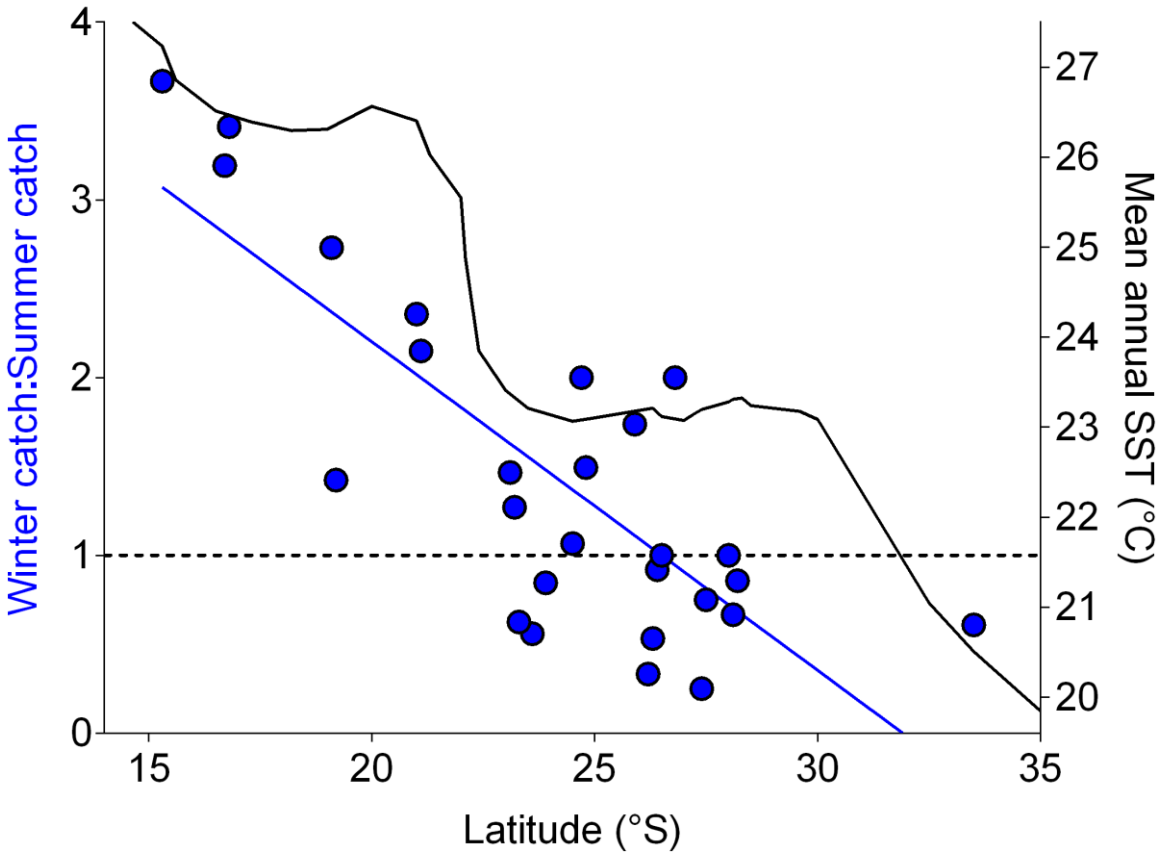


Fig. 1. Temperature dependence of shark catch rates along Australia's eastern coast. Multi-decadal catch data were grouped into four latitudinal zones (inset legend) and presented as percentage catch per calendar month in each zone for (A) tiger sharks *Galeocerdo cuvier*, (B) blacktip sharks *Carcharhinus limbatus* and (C) white sharks *Carcharodon carcharias*. The curve in *A* represents a two-part thermal performance curve, whereas dashed lines in *B* and *C* are fourth-order polynomial curves.



388 **Fig. 2. Shifting seasonality of tiger shark catches along Australia's eastern coast**. Blue
data represent the ratio of total tiger shark catches recorded in winter months (Jun-Aug) to
390 those recorded in summer months (Dec-Feb) at each of 27 locations over multiple decades.
The blue line represents the least squares regression fitted to catch ratios across latitude, and
392 the black line represents mean annual coastal sea surface temperatures across latitude over
the past decade (www.metoc.gov.au). The dashed horizontal line represents the temperature
394 coinciding with maximum tiger shark catches (from Fig. 1a).

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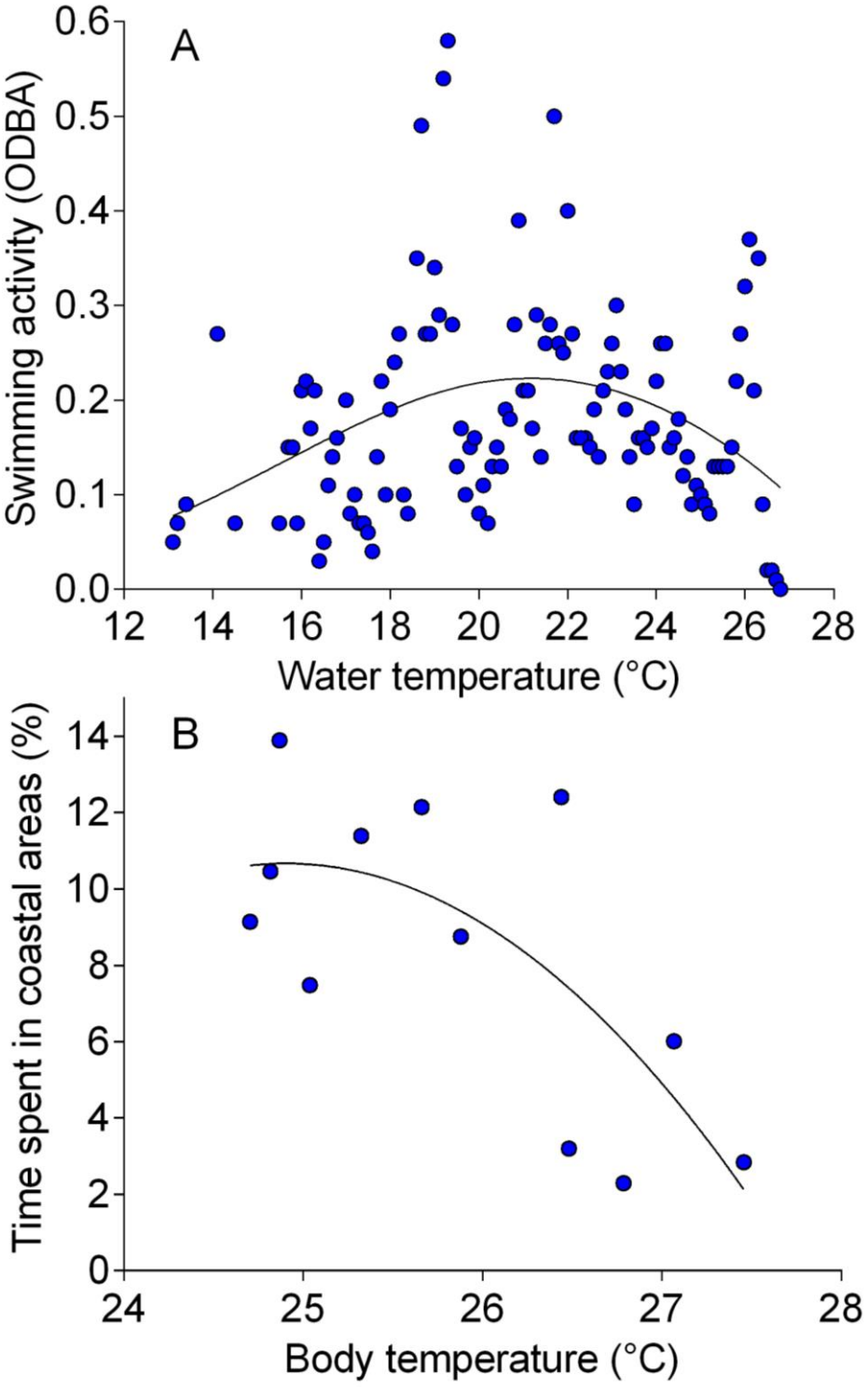

Fig. 3. Swimming activity and body temperature of tiger sharks in coastal Hawaii. (A) Temperature's influence on swimming activity (overall dynamic body acceleration; ODBA) for five free-ranging tiger sharks swimming off the eastern coast of Oahu, Hawaii, for an average of ~ 3 days per shark. ODBA data were rescaled for each shark and grand means calculated per 0.1°C bin across all sharks (see *Methods*), with the black curve representing a two-part thermal performance curve fitted to those data. (B) Grand mean body temperature per calendar month for four tiger sharks internally implanted with temperature sensors and monitored by an array of coastal receivers off Oahu, Hawaii. The y-axis in *B* represents the relative amount of time spent in coastal areas of Hawaii for the corresponding body temperatures.

Discussion

Our combination of diverse datasets reveals temperature can be a powerful indicator of the relative likelihood of both tiger shark coastal occurrences and their activity levels, with both being maximised at the same temperature. The integration of functional trait information is a critical advance over studies that rely solely on correlations between species distributions and environmental conditions, as it suggests tiger sharks may be most abundant in coastal waters of 22°C because they are more active at that temperature. The ultimate cause of the elevated activity levels near 22°C for this species is uncertain; tiger sharks are ectotherms whose maximum power outputs, speeds minimising cost of transport, and minimum cruising speeds will all be influenced by temperature (Iosilevskii & Papastamatiou, 2016), but they are also predators that are likely to be more-active in prey-rich environments. Several other recent studies have measured temperature's influence on growth and activity of wild fishes and found close links with geographical range limits (Neuheimer *et al.*, 2011; Payne *et al.*, 2016). Regardless of the specific pathways by which temperature regulates activity or growth, performance of wild ectotherms may prove a valuable functional trait for informing mechanistic distribution models, and extrapolating projections to future climate scenarios.

Temperature's influence on tiger shark coastal occurrences was pervasive; at any latitude, catches were highest when coastal SSTs were nearest 22°C (Fig. 1a, Fig. S2b). They are thus more likely to be found in coastal areas in winter in the tropics but in summer towards temperate latitudes (Fig. 2). The strength of this seasonal shift is noteworthy because it implies that temperature *per se* is the major determinant of coastal occurrences of the species. There was evidence that Hawaiian sharks showed a similar pattern to Australian sharks, with Hawaiian sharks being more prevalent in coastal waters when temperatures were at their coolest (Fig. 3b). It also appears to hold both on the west coast of Australia (where catches on drum lines in Shark Bay are near zero in coastal water temperatures of 16-17°C,

and generally increase up to maximum summer temperatures of ~ 23-24°C; Heithaus, 2001) and South Africa (where catches at latitudes near the poleward extent of our Australian catch array are highest during the warmest months; Dicken *et al.*, 2016). Further, there is evidence that at least some tiger sharks choose to encounter SSTs of 22°C year-round: two tiger sharks tagged with satellite transmitters off the east coast of Australia (data originally presented in Holmes *et al.*, 2014) were recorded migrating seasonally over approximately 12° of latitude, continuously exposing themselves to SSTs close to 22°C in the process (Fig. 4 . The sharks were fitted with SPOT5 satellite transmitters). While derived from just two individuals, these data offer evidence that a proportion of tiger sharks track latitudinal shifts in the 22°C isotherm, with seasonal migrations up and down the east coast of Australia (a pattern similar to that seen in the northwest Atlantic; Lea *et al.*, 2015) being a plausible mechanism for explaining the strong trends seen in our catch data (Fig. 1a, Fig. 2). The importance of acclimation or regional adaptation to temperature variation is not clear from our data, with relative catch rates being highest at around 22°C regardless of latitude. A similar finding was made for growth rates of several fish species off Australia's coast, with the temperature's maximising growth appearing conserved within-species across broad latitudinal ranges (Payne *et al.*, 2016). Further exploration of this pattern for tiger sharks could come from activity data collected across a range of latitudes.

Taken together, abundance, performance and movement data suggest a persistent thermal optimum of 22°C for this species, and greater confidence that temperature will be a useful mechanistic predictor of future tiger shark populations than would models parameterized by distribution data alone. An important caveat is that elevated shark activity might increase their catchability on drumlines and nets, such that catch rate is somewhat reflective of activity as well as abundance. The proportionality of CPUE to abundance is

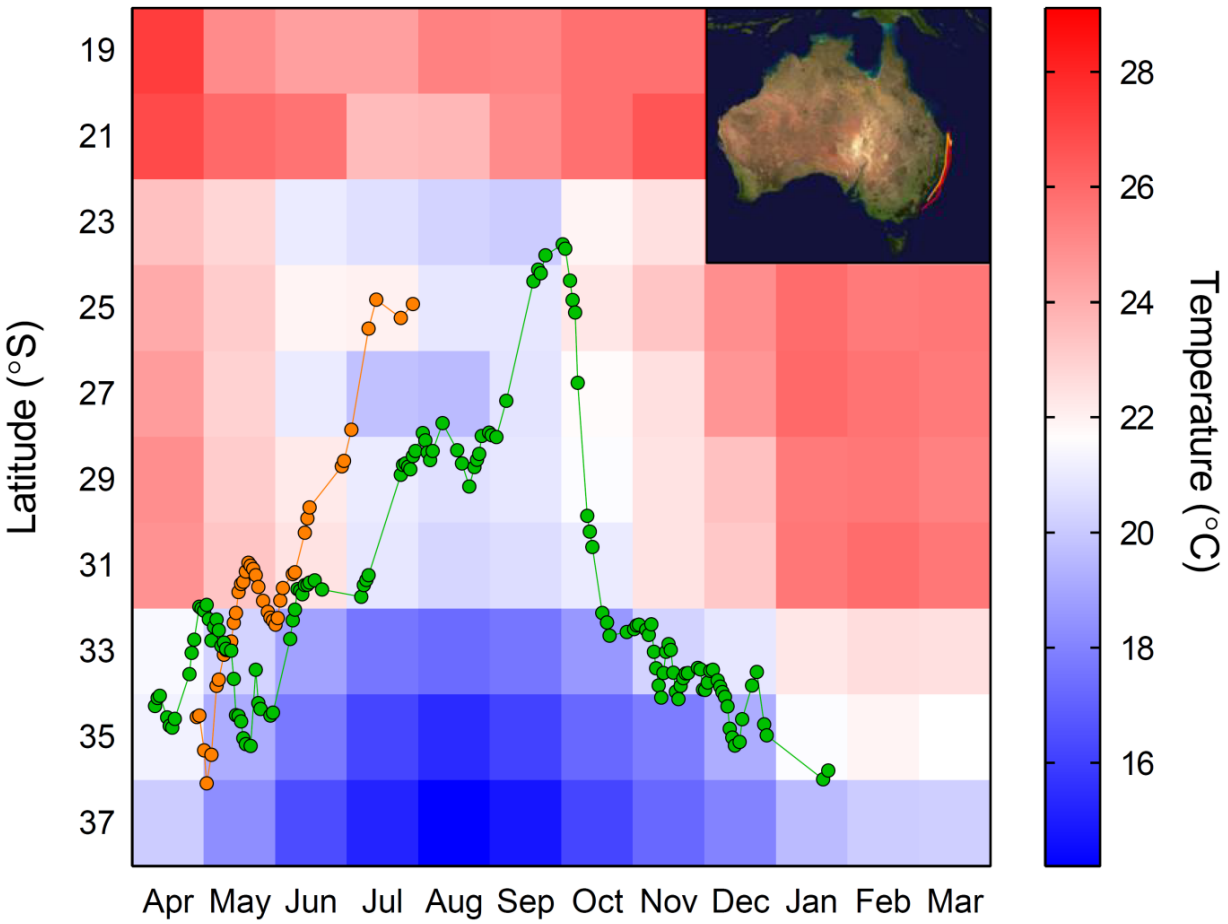

Fig. 4. Tiger sharks tracking their optimal temperature. Green and orange data represent daily latitudinal locations of two tiger sharks (tracks reproduced in inset map) overlaid onto average monthly coastal sea surface temperatures for 10 locations along eastern Australia (SST data from www.metoc.gov.au). White areas indicate the thermal optimum for catch rates and swimming activity (~ 21.5°C) of tiger sharks (this study). Satellite tracking data derived from Holmes *et al* (2014).

long-debated (Harley *et al.*, 2001) and disentangling the influence of shark activity and abundance on catch rate would require independent abundance data (such as from aerial surveys or trawls) that is currently unavailable.

Catch data from Australia and performance data from Hawaii suggest relative coastal abundance and performance are highest near 22°C, yet some tiger sharks in some regions appear to rarely encounter such temperatures. For example, tagged tiger sharks throughout the Hawaiian Islands only spent a small proportion of time in water temperatures below 24°C

across several months (Papastamatiou *et al.*, 2013 and Fig. 3b in this paper). This species clearly has a broad thermal niche, as highlighted by the large temperature range over which tiger sharks were caught and can maintain performance in our study (Fig. 1a, Fig. 3a), and negative fitness impacts associated with inhabiting temperatures outside their optimal range can be buffered by other factors. For example, the annually resident tiger sharks at Raine Island, northern Australia, encounter SSTs of almost 30°C during the summer months, but are rewarded by having access to the highest density green turtle *Chelonia mydas* rookery in the world during this period (Fitzpatrick *et al.*, 2012), and can expend minimal foraging energy there by scavenging (Hammerschlag *et al.*, 2016). So although tiger shark distributions are not constrained by availability of temperatures close to 22°C, our data show that the likelihood of their occurrence and activity levels increases nearer this temperature. The ability of ectotherms to behaviourally buffer deleterious effects of sub-optimal temperatures are becoming increasingly recognised (Kearney *et al.*, 2009; Sunday *et al.*, 2014), and is an important consideration when forecasting tiger shark distribution shifts, particularly at range boundaries. For example, the acoustically-tagged Hawaiian sharks were still detected over the warmest months (Fig. 3b), but need not travel far to have access to cooler habitat at depth, as other sharks are known to seek out (Sims *et al.*, 2006).

Human encounters with potentially dangerous shark species are an increasingly contentious socio-political issue, and have motivated recent research seeking to identify the most important risk factors (such as the type of ocean activity undertaken by humans; Ferretti *et al.*, 2015) influencing the likelihood of attacks. Beyond the implications of our results for understanding the distribution of tiger sharks, it is important to note that revealing the temperature at which this species is most active may also have implications for predicting the likelihood of shark bites. Our current understanding of the ultimate mechanisms influencing variability in shark attack frequency is poor (Ferretti *et al.*, 2015), so it is unclear whether

524 more-active sharks are more likely to bite humans. Our accelerometry results could provide impetus for future studies exploring the mediating role of activity levels in any links between
526 temperature and the likelihood of shark attacks. Accounting for variability in the behaviour of both humans (e.g. Ferretti *et al.*, 2015) and sharks could provide for the most informed shark
528 management programs.

530 *Conclusion*

The integration of performance and abundance data makes an important step toward a
532 mechanistic understanding of how temperature regulates tiger shark distributions, and highlights the usefulness of temperature as a predictor for models linking distribution with
534 fitness and performance. Models based solely on temperature may be of great benefit to management programs wishing to provide easily understood metrics relating shark
536 occurrences to their environment, as compared to species distribution models underpinned by multivariate predictors. Our data suggest that tiger sharks are willing to move in response to
538 (or alongside) patterns in SST, and that they will be a species whose spatial distribution responds to future changes in SST. We would also expect a southward shift in the latitude at
540 which winter and summer occurrences are similar; a further ~1-2°C warming could see beaches around Sydney (some of the most popular in the country for bathers) hosting tiger
542 sharks in similar abundances in both summer and winter (Fig. 2). SST might be a better predictor of tiger shark range extensions (into temperate regions) rather than complete
544 distribution shifts, which (given their current broad temperature range in tropical regions) will likely be buffered by complex biogeographical processes. Indeed, the past decade has
546 seen tiger sharks observed off the northern coast of Tasmania (41°S) – a global warming 'hotspot' – for the first time in recorded history (Last *et al.*, 2011), and while most global
548 populations of the species have declined in recent decades (Baum *et al.*, 2003; Holmes *et al.*,

2012) catches of tiger sharks off the temperate coast of South Africa have increased (Dicken
550 *et al.*, 2016), consistent with a poleward distribution shift. Recent climate change scenarios predict further increases in summer SSTs of ~1°C by the middle of this century in the waters
552 off south eastern Australia, so it would be unsurprising if tiger sharks became more prevalent in that region in coming decades; particularly since average summer temperatures in the
554 region of the recent tiger shark encroachments to northern Tasmania (~ 17-18°C; www.metoc.gov.au) match the lower temperature limit in which the species is caught
556 throughout Australia's bather protection program (Fig. 1a).

Shifts in the distribution of sharks in coastal areas is an important socio-political
558 issue, and one often cited with a perception of an increasing likelihood of shark bites on humans in recent decades (Ferretti *et al.*, 2015). Incorporating seasonal trends in water
560 temperature into bather protection programs may simultaneously improve public safety and reduce ecological impacts of shark removal programs, because being able to predict when
562 and where potentially dangerous sharks are both most active and most likely to occur in coastal zones could facilitate dynamic management programs that do not simply rely on
564 killing sharks. For example, the Queensland government in Australia has reduced incidences of bather injury caused by dangerous cubozoans through public awareness campaigns aimed
566 at educating the general public as to when and where those species occur across the State. A similar approach to shark management could have the broadest benefits.

568

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Supplementary Material

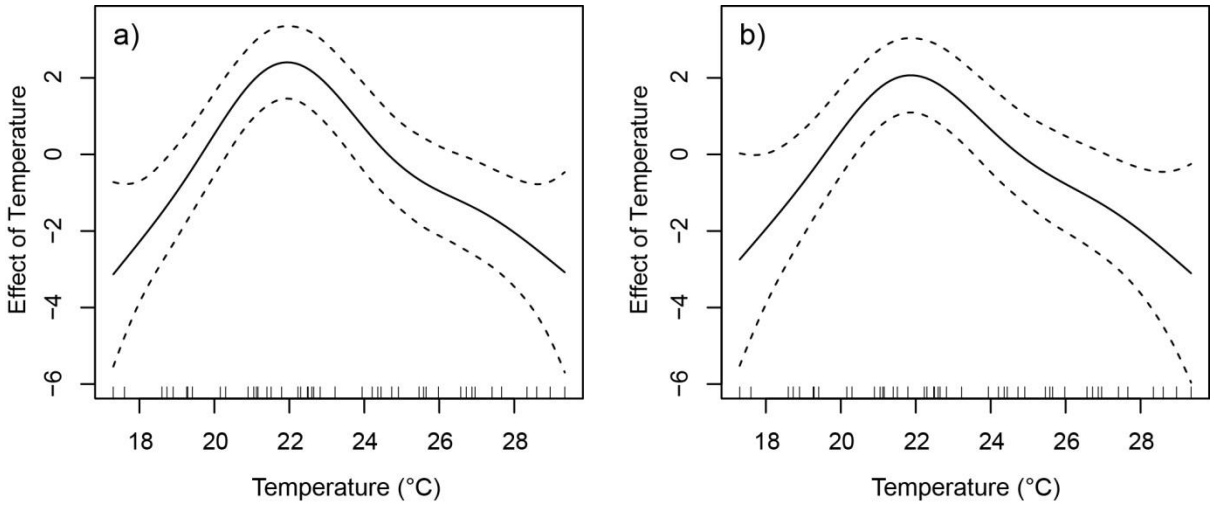

Fig. S1. a) Fitted temperature smoother in the GAM of % catch data. b) Fitted temperature smoother in the GAMM of % catch data. The GAM included a smoother for 'temperature', and the GAMM included an additional cyclic smoother for 'month', and an autoregressive term (AR1) for 'month' nested in 'zone'.

Table S1. Results of the smoother terms in the GAM and GAMM fitted to the % catch data (Fig. S1). The fitted models are given in script notation, where 's' refers to the smoothing function. The AR1 term does not account for the correlation between December and January, but the cyclic smoother of month does.

	edf	*F*	*P*
Model: *% Catch* ~ s(*Temp*)			
s(Temp)	4.1	6.45	0.0001
Model: *% Catch* ~ s(*Temp*) + s(*Month*, bs='cc'), corAR1(~*Month*|*Zone*)			
s(Temp)	3.6	5.25	0.002
s(Month)	0.3	0.04	0.313

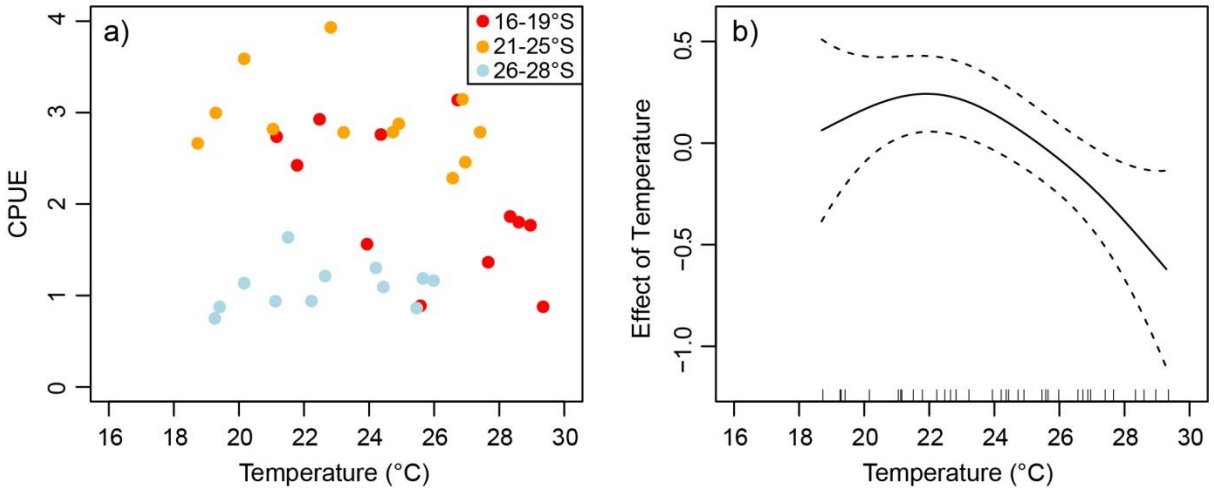

Fig. S2a-b. a) The tiger shark catch-per-unit-effort (CPUE; sharks drumline^{-1} day^{-1}). b) Fitted temperature smoother in the GAM of CPUE data in (a).

Table S2. Results of the GAM fitted to the CPUE data (Fig. S2b).

Model: *CPUE* ~ s(*Temp*) + Zone				
	Estimate	S.E.	*t*	*P*
Intercept	2.15	0.15	14.2	< 0.001
Zone 2	0.75	0.21	3.5	0.001
Zone 3	-1.18	0.22	-5.3	< 0.001
	edf	*F*	*P*	
s(Temp)	2.1	3.0	0.04	

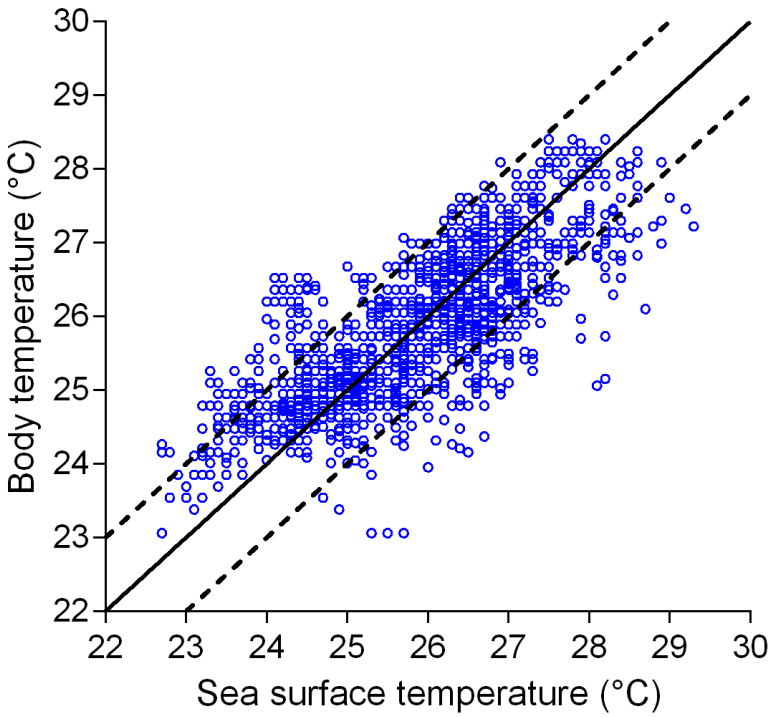

Fig. S3. Relationship between hourly recorded SST (Kahului Harbor, Maui https://tidesandcurrents.noaa.gov) and mean hourly internal body temperatures of four tiger sharks implanted with temperature sensors and monitored in coastal regions of Maui from October 2013 to June 2015. Body temperatures generally matched corresponding SSTs (solid line represents xy unity), with 85% of hourly body temperature readings falling within ± 1.0°C of SSTs throughout the 33 month monitoring period.